

## Inorganic Nutrient Fluxes in Anemone-dominated Tide Pools<sup>1</sup>

SUSAN L. JENSEN<sup>2,3</sup> AND GISELE MULLER-PARKER<sup>2,4</sup>

**ABSTRACT:** Physical and chemical characteristics of seawater in two natural tide pools on Rosario Beach, Fidalgo Island, Washington, were compared during midday low tides in July 1991. One pool contained a mixed assemblage of macroalgae (40% cover) and invertebrates (50% cover). The second pool was dominated (75% cover) by the sea anemone *Anthopleura elegantissima* (Brandt, 1835), which contains symbiotic algae (zooxanthellae). Temperature, salinity, dissolved oxygen, and pH levels increased in both pools with irradiance and length of emersion. The resident organisms caused changes in the inorganic nutrient levels of the tide-pool seawater. *Anthopleura elegantissima* released substantial amounts of ammonium;  $\text{NH}_4^+$  in the anemone-dominated pool increased by 33% whereas  $\text{NH}_4^+$  declined in the mixed assemblage pool by an average of 28%. Nitrate and nitrite declined in both pools, whereas phosphate remained constant during the 6-hr sampling periods.  $\text{NH}_4^+$  release by *A. elegantissima* was confirmed in studies of artificial tide pools, where  $\text{NH}_4^+$  levels increased by an average of 71% over an 8-hr period. Release of ammonium by *A. elegantissima* under natural conditions in the field provides a contrast to nutrient fluxes observed for tropical symbiotic associations.

THE TIDE POOL is a dynamic ecosystem, changing with the ebb and flow of the tides. At high tide the pools are submerged, the water is continuously exchanged, and the system remains open. When the tide recedes, the tide pool is suddenly isolated and becomes a closed ecosystem for different periods of time. Although tide-pool organisms remain in an aquatic environment during low tides, they may be subjected to large temperature and salinity changes, as well as fluctuations in dissolved inorganic materials such as ammonium, nitrate, nitrite, phosphate, and oxygen (Klugh 1924, Ganning 1971). The physical

and chemical changes of seawater in tide pools during emersion periods have been examined in numerous studies (Stephenson et al. 1934, Newell 1970, Truchot and Duhamel-Jouve 1980, Morris and Taylor 1983, Huggett and Griffiths 1986). However, with the exception of study of oxygen and carbon dioxide changes associated with differences in primary production in animal and algae tide pools (Stephenson et al. 1934), none have targeted specific tide-pool inhabitants to examine their effect on the seawater in the tide pool. Changes in the inorganic nutrients during emersion periods may provide new information about the tide-pool organisms.

*Anthopleura elegantissima* (Brandt, 1835) is a temperate sea anemone that is abundant in the intertidal zone along the coast of the northeastern Pacific Ocean (Hand 1955). These anemones contain photosynthetic symbiotic algae (zooxanthellae) that are highly productive; gross production by *A. elegantissima* is comparable with that of intertidal macroalgae on an areal basis (Fitt et al. 1982). Tropical and temperate algal-cnidarian sym-

<sup>1</sup> This research was funded by an NSF REU Site award (OCE-9000676) to Shannon Point Marine Center and by OCE-8996242 to G.M.P. Manuscript accepted 7 December 1992.

<sup>2</sup> Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, Washington 98221.

<sup>3</sup> Current address: Department of Biology, University of South Florida, Tampa, Florida 33620-5150.

<sup>4</sup> Author to whom requests for reprints should be addressed.

bioses differ with respect to the supply of zooplankton food and the nutrient content of the seawater, both of which are much higher in the temperate waters of the northeastern Pacific Ocean. Studies of tropical symbiotic corals have shown that inorganic nutrients are taken up and retained within the symbiosis by the zooxanthellae (D’Elia 1977, Muscatine and D’Elia 1978, Szmant et al. 1990). Furthermore, nitrogen and phosphorus exchanges between symbiotic invertebrates and seawater are related to the feeding history of the host. Well-fed hosts release both ammonium (Szmant-Froelich and Pilon 1984) and phosphate (Muller-Parker et al. 1990) into the seawater environment as waste products. In contrast to tropical symbioses, there is no information about the nutrient fluxes between *A. elegantissima* and seawater. These symbiotic anemones, having more available food, may feed more frequently than symbiotic corals, thus releasing more nutrients as waste metabolites. The effect of *A. elegantissima* on the nutrient changes in the ambient seawater of the tide pool is explored by a comparison of the physical parameters and nutrient fluxes of a mixed-assemblage pool and an anemone-dominated pool, using additional artificial tide pools containing only

*A. elegantissima*. If feeding by *A. elegantissima* results in a greater release of nutrients into the ambient seawater, this should be detected in tide pools containing these anemones.

MATERIALS AND METHODS

Tide Pools

Two natural rock tide pools at Rosario Beach, Washington, on Fidalgo Island (122°39’50” N, 48°25’14” W) were each sampled on three consecutive days in July 1991, during low tides that exposed these pools during the midday period. Both pools were formed by the retention of seawater in natural depressions, and there was no groundwater input. Tide pool 1 was selected as a representative pool of the midintertidal zone, because it contained a diverse assemblage of macroalgae, invertebrates, and fish. Tide pool 2 was chosen for its large number of *A. elegantissima*. Percentage cover by the different organisms was assessed by placing a 0.25-m<sup>2</sup> quadrat over the pool and measuring the areal distribution of dominant classes of organisms as viewed from above the pool. Table 1 lists

TABLE 1  
CHARACTERISTICS OF NATURAL TIDE POOLS AT ROSARIO BEACH, WASHINGTON, DURING JULY 1991

CHARACTERISTICS	TIDE POOL 1	TIDE POOL 2
Pool area (m)	1.6 by 2.1	1.3 by 1
Pool volume (liters)	43	30
Tidal height [ft (m)]	2.3 (0.7)	5.1 (1.55)
Species present (% cover)		
Macroalgae	(40%) <i>Fucus gardneri</i> Silva <i>Leathesia difformis</i> (Linnaeus) Areschoug <i>Ulva</i> sp. <i>Endocladia muricata</i> (Postels & Ruprecht) Agardh	(<1%) <i>Cladophora</i> sp.
Invertebrates	<i>A. elegantissima</i> (25%) <i>Balanus glandula</i> Darwin (15%) <i>Pagurus hirsutiusculus</i> (Dana) <i>Hemigrapsus nudus</i> (Dana) <i>Collisella pelta</i> (Rathke) (10%)	<i>A. elegantissima</i> (75%) <i>Balanus glandula</i> (10%) <i>Littorina</i> sp. (2.5%) <i>Nucella emarginata</i> (Deshayes) (2.5%) <i>Collisella pelta</i> (10%)
Vertebrates	<i>Oligocottus maculosus</i> Girard (sculpin)	

the physical characteristics and the resident organisms of each tide pool. A third set of artificial tide pools containing only *A. elegantissima* was sampled on 2 days in August 1991. The artificial tide pools were round (40 cm diam.), shallow, plastic bowls that held 3.8 liters of seawater. Sixty-four anemones were placed into each of two artificial tide pools. Anemones for the artificial tide pools were collected on 3 August 1991 at Skyline Beach, Anacortes, Washington, at an approximate tidal height of 1.5 ft. (0.46 m). A third artificial tide pool containing only seawater (4.6 liters) served as a control. The artificial tide pools were exposed to unshaded natural light outside and were sampled on 7 and 10 August 1991. Between days of sampling, pools were kept submerged in a flow-through seawater system at ambient temperature (12°C).

#### Data Collection

Tidal heights of pools were established using a surveying level, a stadia rod, and a reference tidal height at the water's edge. Temperature, salinity, dissolved oxygen, and irradiance were measured in situ at one site in the middle of each tide pool. Temperature was measured with a mercury thermometer, salinity with a temperature-compensated refractometer (Reichert-Jung, Cambridge Instruments, Buffalo, New York), and dissolved oxygen with an oxygen probe (Model 57, Yellow Springs Instr. Co., Yellow Springs, Ohio) and meter. Irradiance was measured with a  $4\pi$  underwater quantum sensor connected to a datalogger (LI-1000, LI-COR, Inc., Lincoln, Nebraska); irradiance data averaged over 15-min intervals were subsequently downloaded to a computer. Nutrient concentrations within the tide pools were monitored by taking seawater samples from the tide pools with an acid-washed 30-ml syringe and filtering the sample through a GF/F (Whatman International, Maidstone, England) filter (nominal pore size  $0.7\ \mu\text{m}$ ) held in a Gelman (Gelman Sciences Inc., Ann Arbor, Michigan) filter holder. Filtered water samples were placed in acid-washed polyethylene bottles and kept on ice until brought back to the laboratory (within 2–7 hr). Sea-

water samples were also collected from the ocean for comparison with tide-pool samples. At the laboratory, 10 ml was removed from each sample for determination of pH (Parsons et al. 1984), and the remainder was frozen at  $-15^\circ\text{C}$ . Samples were thawed immediately before analysis of nutrients.

The samples were analyzed for ammonium ( $\text{NH}_4^+$ ) by the phenol-hypochlorite method and phosphate ( $\text{PO}_4^{3-}$ ) as specified in Parsons et al. (1984). Both analyses were scaled for a 5-ml sample size, and absorbance of the final products was measured on a diode array spectrophotometer (Hewlett-Packard 8452). Combined nitrate and nitrite of samples was measured with an autoanalyzer using a cadmium reduction column (Parsons et al. 1984) and an autoanalyzer (ALPKEM RFA 300, Perstorp Analytical, Wilsonville, Oregon) (RFA method: nitrate + nitrite-nitrogen, no. A303-S170).

The artificial pools were placed at ground level outdoors in an unshaded area protected from the wind near the laboratory at the start of each sampling period. The pools were sampled during the same time of day as the natural pools, but there was no delay between removal of the pools from the flow-through seawater system and the first pool measurements. All sampling procedures were similar, except that the pH was measured immediately after collection, and the water samples were frozen within 10 min of collection. Irradiance was measured in the control pool and was assumed to be the same for all three pools. Salinity, temperature, and dissolved oxygen were measured in each of the three pools.

## RESULTS

### Tide Pool 1

Tide pool 1 (see Table 1) was isolated from the ocean for 3 hr, 20 min; 3 hr, 10 min; and 2 hr, 50 min, respectively, on 10, 11, and 12 July before sampling began. Temperature increased linearly from  $14^\circ\text{C}$  to a maximum value of  $31^\circ\text{C}$  at 1500 hr on 12 July, and salinity rose from 29 to 31‰. Underwater

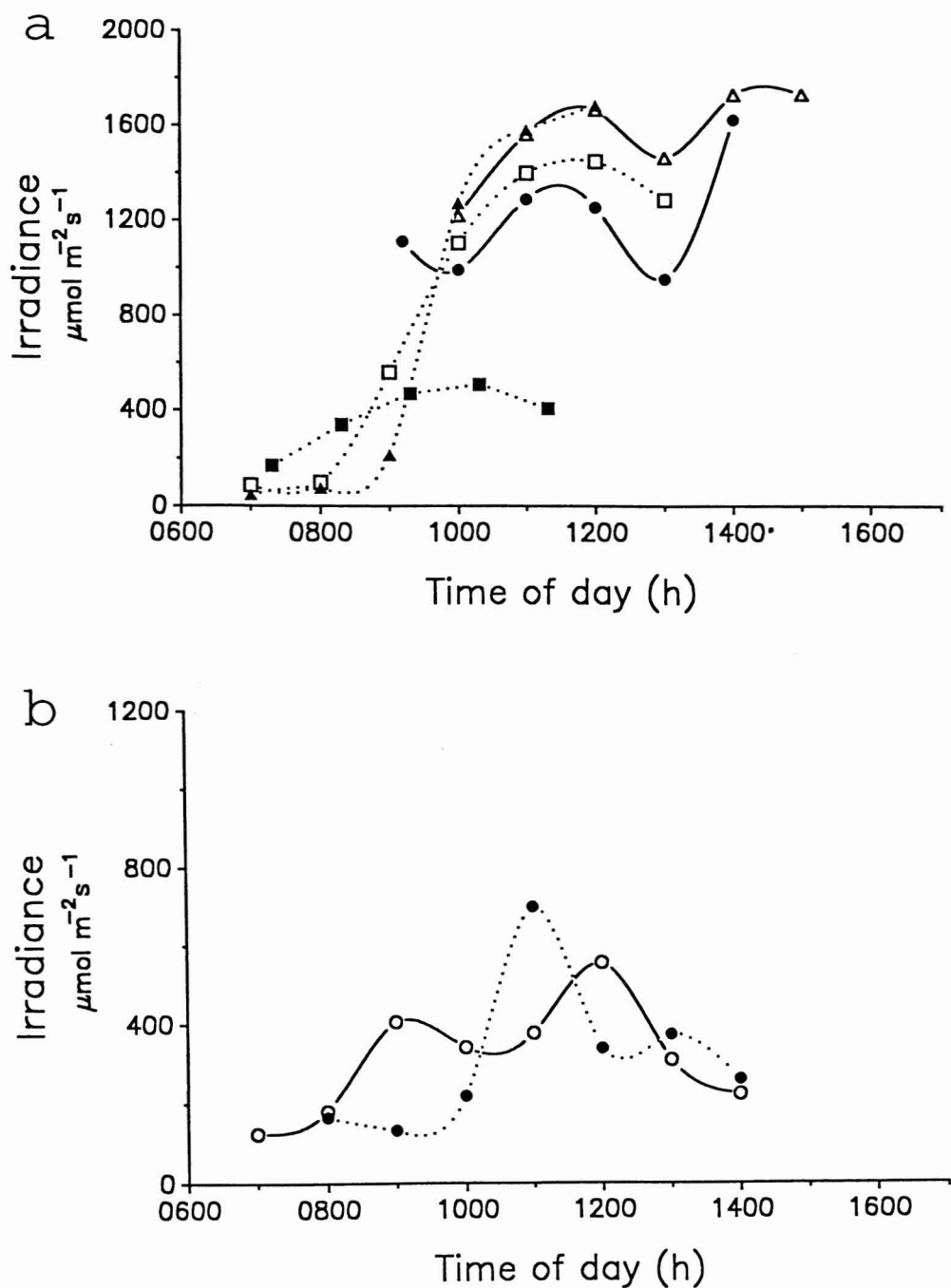


FIGURE 1. Irradiance in the natural and the artificial tide pools at Rosario Beach, Washington, 1991: (a) Natural tide pools. Tide pool 1 data are connected by solid lines and tide pool 2 data by dotted lines. Pool 1 was sampled 11 (●) and 12 July (Δ). Light data for pool 1 on 10 July are missing. Pool 2 was sampled 22 (▲), 23 (□), and 24 July (■). (b) Artificial tide pools. Light data collected 7 August are connected by the solid line (○) and light data from 10 August by the dotted line (●).

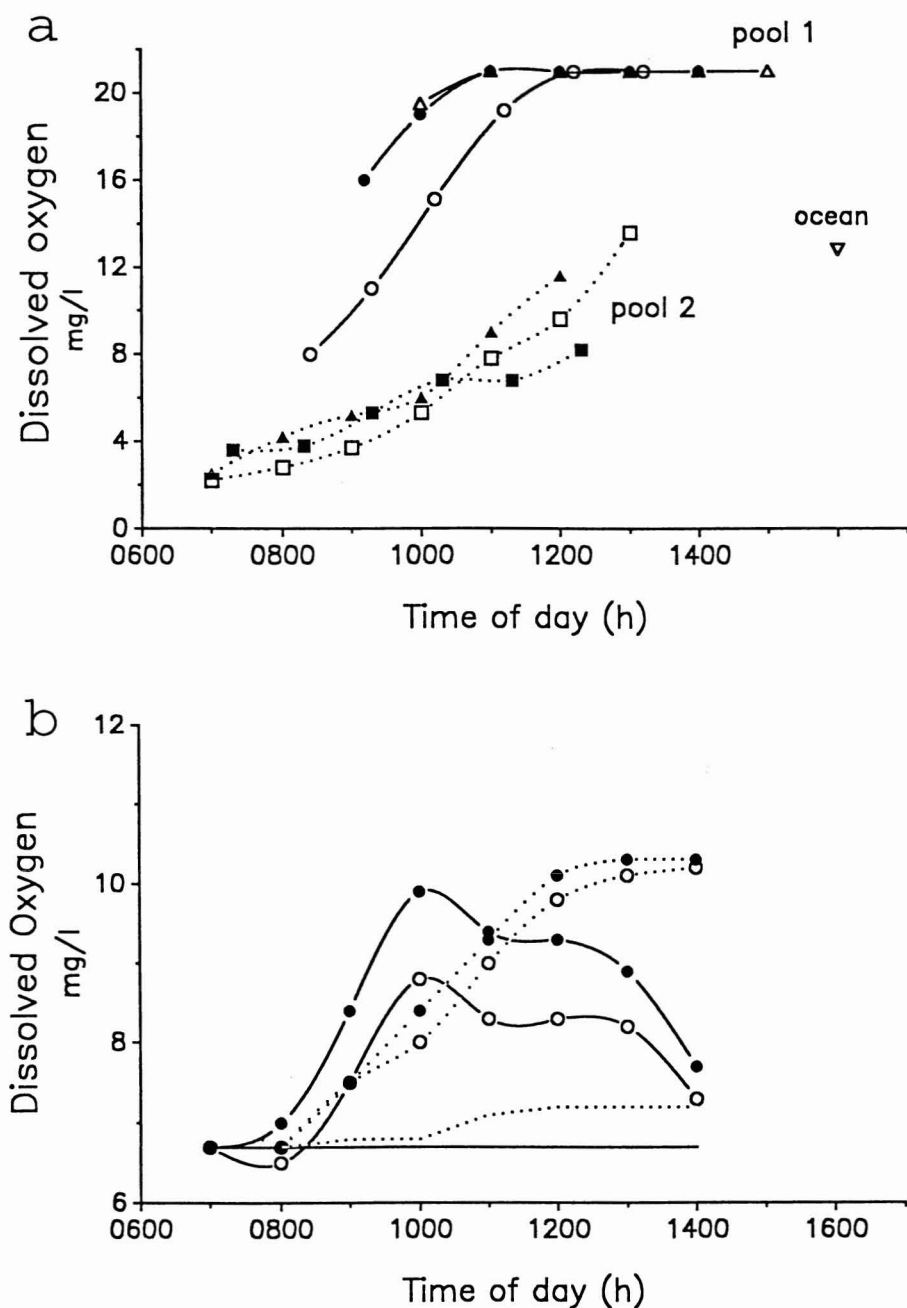


FIGURE 2. Dissolved oxygen in the natural and the artificial tide pools at Rosario Beach, Washington, 1991: (a) Natural tide pools. Tide pool 1 data are connected by solid lines and tide pool 2 data by dotted lines. Pool 1 was sampled 10 (○), 11 (●), and 12 July (Δ). Pool 2 was sampled 22 (▲), 23 (□), and 24 July (■). Dissolved oxygen concentration of the adjacent ocean is indicated by the ▽ symbol ( $\pm$  SE, obscured by symbol). (b) Artificial tide pools. Data collected 7 August are connected by the solid lines and data from 10 August by the dotted lines. Pool A (○) and pool B (●) contained 64 *A. elegantissima* each; the control pool data for each date are indicated by the lines without symbols.

irradiance increased from 50 to 1600  $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  (Figure 1a). Dissolved oxygen increased from 8 mg/liter to supersaturated concentrations (Figure 2a) that were also noted by the presence of oxygen bubbles. The pH increased an average of 1.08 units over the 7-hr time course of measurements, from an initial value of 7.5 to 8.6. Dissolved inorganic nitrogen levels declined in the tide pool during the day. Ammonium levels dropped from 1.8 to 1.0  $\mu\text{M}$ , but remained close to concentrations determined for the adjacent ocean seawater (Figure 3a). Combined nitrate and nitrite levels also decreased with time on each of the 3 days (Figure 4a). Phosphate levels were variable and decreased only slightly, the largest change taking place on 11 July, from 2.4 to 1.7  $\mu\text{M}$  (Figure 5a).

#### *Tide Pool 2*

Sampling began 4 hr, 30 min; 4 hr, 5 min; and 3 hr, 35 min after the pool was isolated by the ebb tide on 22, 23, and 24 July, respectively. Temperature rose from 13°C to the maximum value of 26°C at 1300 hr on 23 July, and salinity and underwater irradiance (Figure 1a) increased as in the first pool, except for 24 July, which was a cloudy day (Figure 1a). Dissolved oxygen increased with irradiance, but the increase was more gradual than in tide pool 1, going from 2.2 mg/liter to near seawater levels by 1300 hr (Figure 2a). Initial pH values were low (pH = 6.9) relative to that of the ocean (pH = 7.3). The pH did not exceed 7.5 at any other time. In contrast to tide pool 1, levels of both ammonium and phosphate increased with time. Ammonium concentrations in tide pool 2 were an order of magnitude greater than that of the adjacent seawater, starting at 12.2  $\mu\text{M}$  and attaining 18.3  $\mu\text{M}$  on 24 July (Figure 3a). Phosphate levels were also higher in the tide pool. Phosphate increased from an initial concentration of 3.6  $\mu\text{M}$  to 6.5  $\mu\text{M}$  on 24 July (Figure 5a). Nitrate and nitrite concentrations were higher than those obtained in tide pool 1 and in the adjacent seawater (Figure 4a), although there was a similar decline in both pools during the sampling period.

#### *Artificial Tide Pools*

The differences in the nutrient fluxes observed in the two natural tide pools suggested that the anemones in tide pool 2 released considerable quantities of dissolved inorganic nutrients ( $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$ ). To test the effect of *A. elegantissima* on seawater nutrient levels, two artificial tide pools (A and B) with anemones as the sole inhabitants were compared with a control artificial pool containing only unfiltered seawater. The artificial tide pools showed trends similar to those of the two natural tide pools with respect to temperature and salinity. However, physical conditions were very different during this set of experiments because the sky was continually overcast; irradiance in the artificial tide pools did not exceed 700  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  (Figure 1b), and the water temperature peaked at 26°C. Salinity levels remained constant (30‰), presumably because of lower temperatures and little exposure to wind at the sampling site. Dissolved oxygen levels rose on both days; on 7 August it reached a maximum of 10 mg/liter at 1000 hr in the two anemone pools before decreasing, whereas on 10 August oxygen levels continued to rise throughout the day, reaching 10 mg/liter in the anemone pools, but remaining constant in the control pool (Figure 2b). The pH level increased slightly (from 7.16 to 7.81 in pool A, 7 August), but tended to fluctuate rather than increase steadily. Nutrient concentrations confirmed that the high level of  $\text{NH}_4^+$  observed in tide pool 2 was due to the presence of the anemones.  $\text{NH}_4^+$  increased in the artificial pools containing the anemones, reaching higher levels on the first sampling date (from an initial 0.7  $\mu\text{M}$  to a final 11.4  $\mu\text{M}$  in pool A) and increasing more rapidly on 7 August than on 10 August (0.9 to 3.2  $\mu\text{M}$ , Figure 3b). Ammonium levels in the control pool remained constant. Phosphate showed little, if any, increase, fluctuating within the range of 2.0 to 3.0  $\mu\text{M}$  on both days (Figure 5b). Phosphate levels in the control pool remained constant on 7 August and rose slightly on 10 August. Seawater concentrations of nitrate and nitrite remained constant in the control

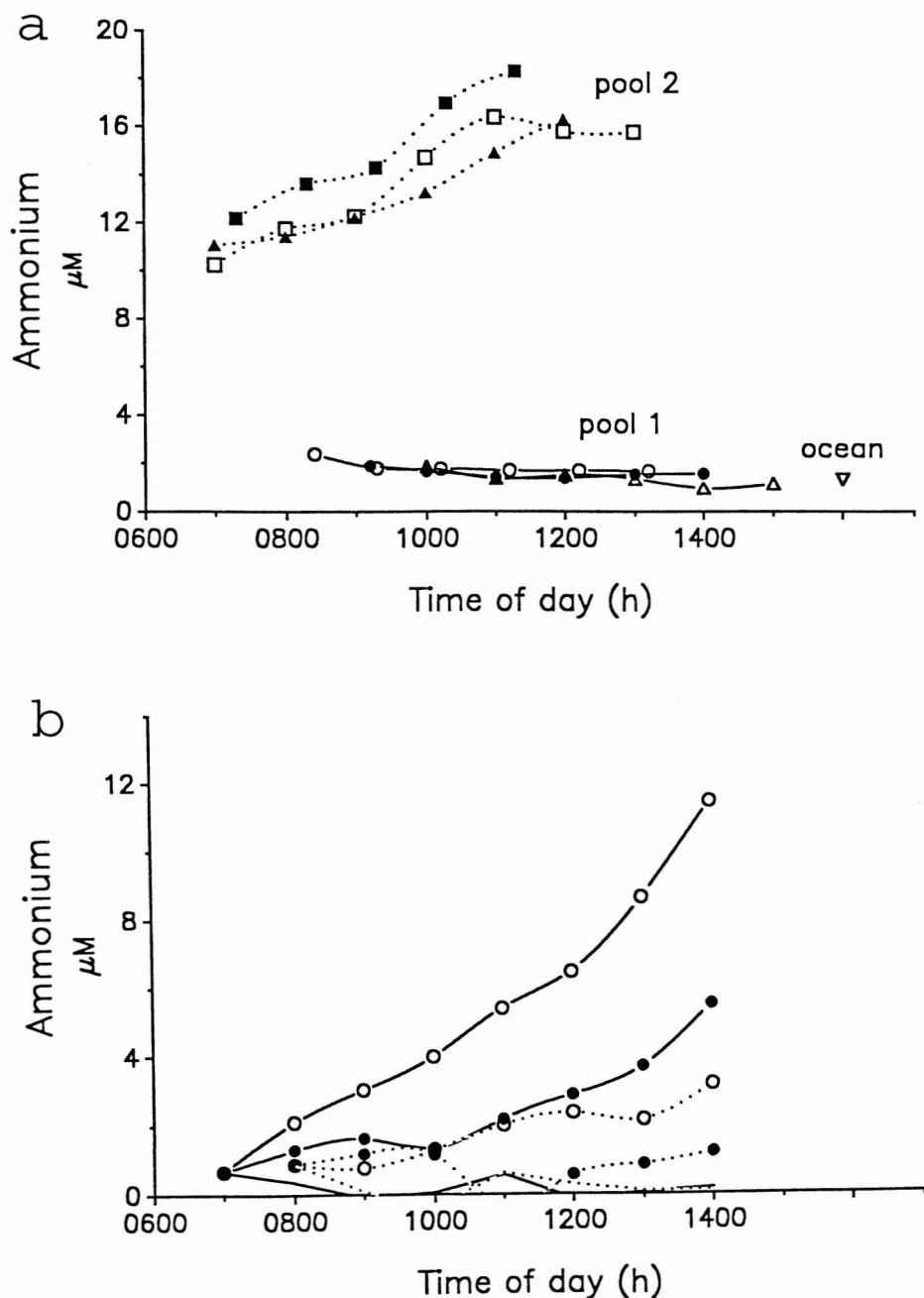


FIGURE 3. Seawater ammonium concentrations in the natural and the artificial tide pools at Rosario Beach, Washington, 1991: (a) Natural tide pools. Tide pool 1 data are connected by solid lines and tide pool 2 data by dotted lines. Pool 1 was sampled 10 ( $\circ$ ), 11 ( $\bullet$ ), and 12 July ( $\Delta$ ). Pool 2 was sampled 22 ( $\blacktriangle$ ), 23 ( $\square$ ), and 24 July ( $\blacksquare$ ). Seawater ammonium is indicated by the  $\nabla$  symbol ( $\pm$  SE, obscured by symbol). (b) Artificial tide pools. Data collected 7 August are connected by the solid lines and data from 10 August by the dotted lines. Pool A ( $\circ$ ) and pool B ( $\bullet$ ) contained 64 *A. elegantissima* each; the control pool data for each date are indicated by the lines without symbols.

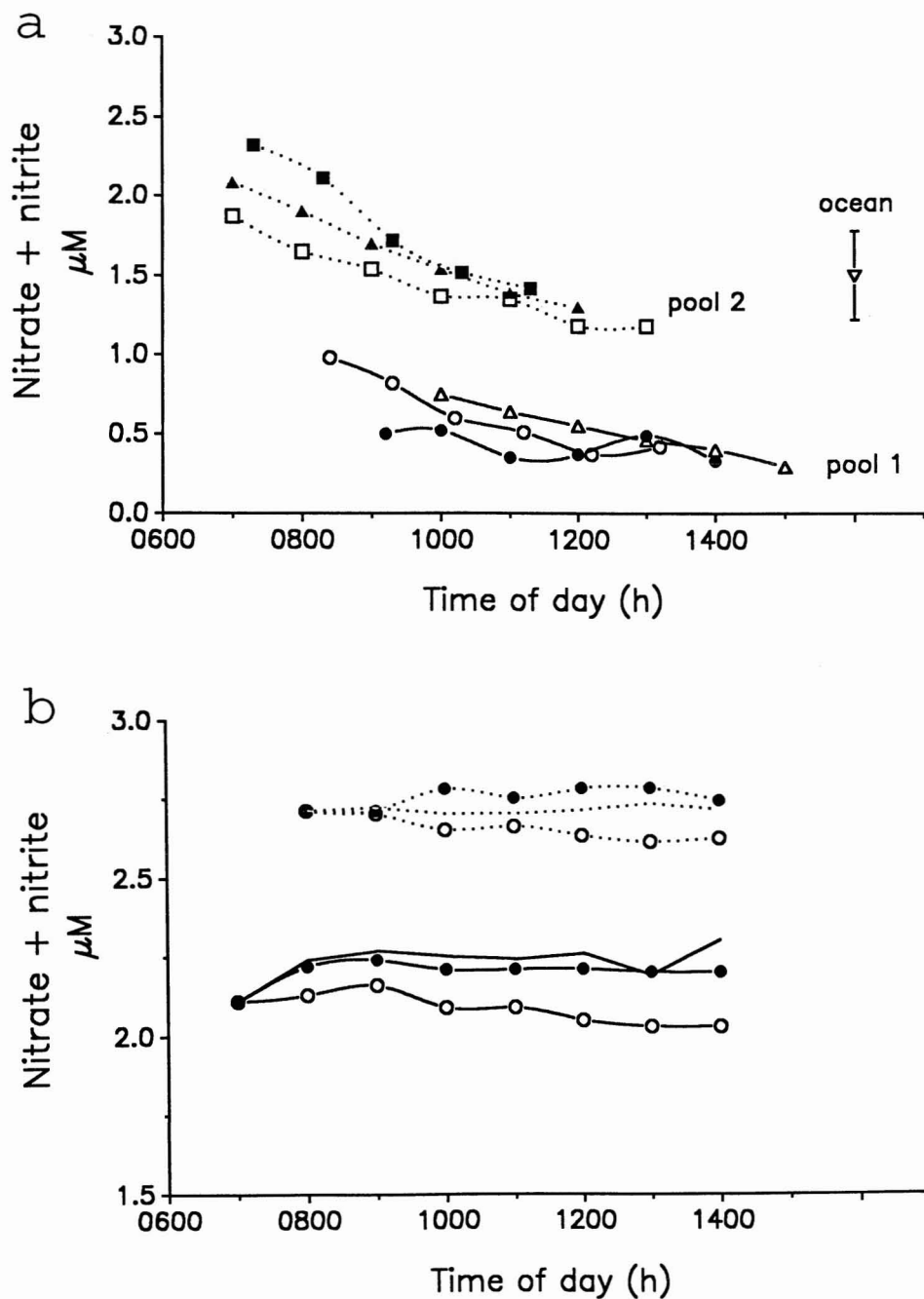


FIGURE 4. Seawater combined nitrate and nitrite concentrations in the natural and the artificial tide pools at Rosario Beach, Washington, 1991: (a) Natural tide pools. Tide pool 1 data are connected by solid lines and tide pool 2 data by dotted lines. Pool 1 was sampled 10 (○), 11 (●), and 12 July (Δ). Pool 2 was sampled 22 (Δ), 23 (□), and 24 July (■). Seawater concentrations are indicated by the ▽ symbol ( $\pm$  SE). (b) Artificial tide pools. Data collected 7 August are connected by the solid lines and data from 10 August by the dotted lines. Pool A (○) and pool B (●) contained 64 *A. elegantissima* each; the control pool data for each date are indicated by the lines without symbols.



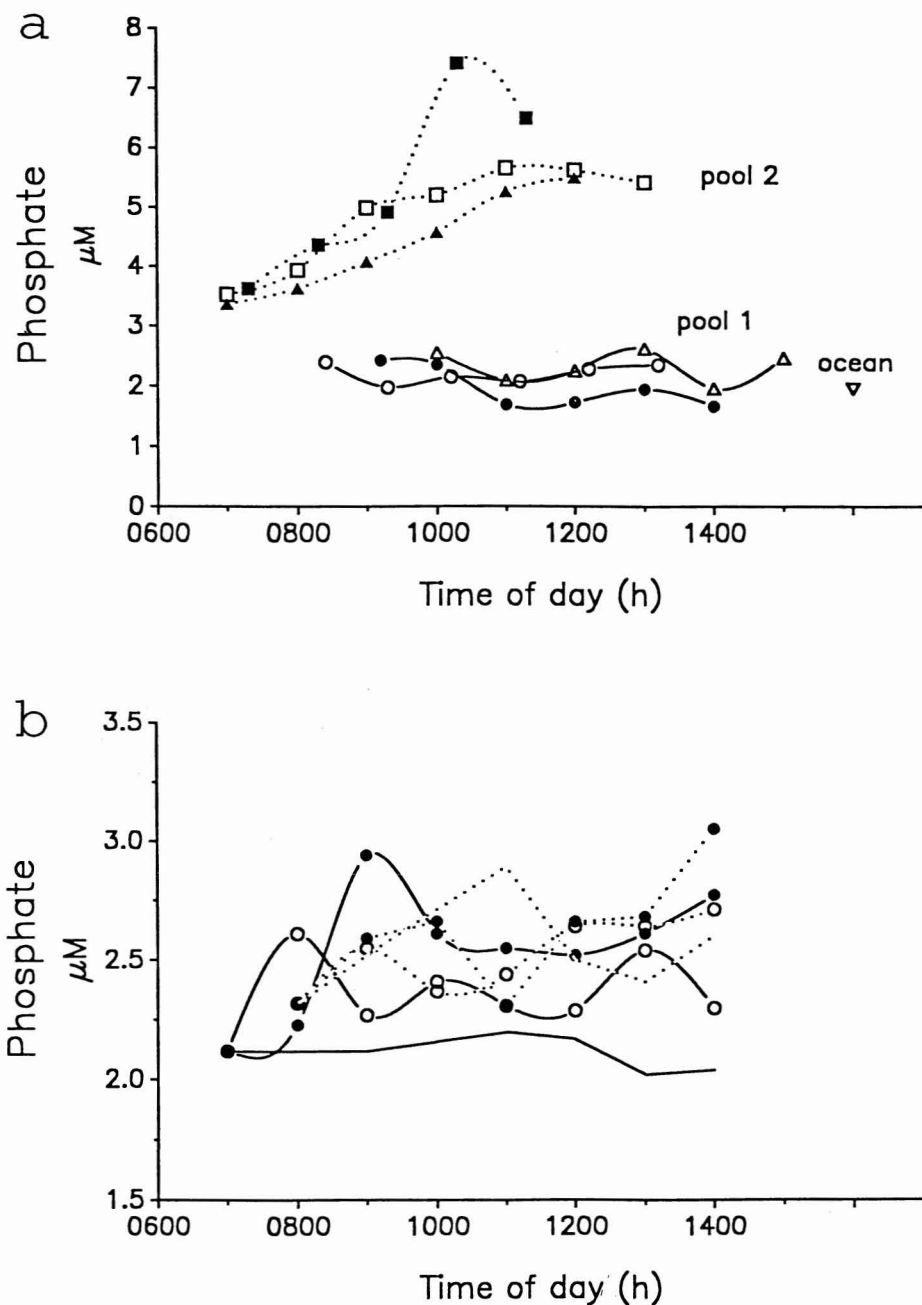


FIGURE 5. Seawater phosphate concentrations in the natural and the artificial tide pools at Rosario Beach, Washington, 1991: (a) Natural tide pools. Tide pool 1 data are connected by solid lines and tide pool 2 data by dotted lines. Pool 1 was sampled 10 ( $\circ$ ), 11 ( $\bullet$ ), and 12 July ( $\Delta$ ). Pool 2 was sampled 22 ( $\blacktriangle$ ), 23 ( $\square$ ), and 24 July ( $\blacksquare$ ). Seawater concentrations are indicated by the  $\nabla$  symbol ( $\pm$  SE, obscured by symbol). (b) Artificial tide pools. Data collected 7 August are connected by the solid lines and data from 10 August by the dotted lines. Pool A ( $\circ$ ) and pool B ( $\bullet$ ) contained 64 *A. elegantissima* each; the control pool data for each date are indicated by the lines without symbols.

pool and in the two pools with *A. elegantissima* (Figure 4b).

#### DISCUSSION

The changes in the inorganic nutrient concentrations in the two natural tide pools are related to the differences in the species composition of each pool. The seawater in tide pool 1, which contained substantial algal cover (Table 1), showed the influence of algal activity overriding that of the resident animals in the following ways. High rates of primary productivity related to increased irradiance during midday emersion resulted in high levels of dissolved oxygen and high pH. The concentration of dissolved inorganic nitrogen decreased with time, indicating net algal nutrient uptake of the nutrients produced as metabolites by the animal population. In contrast, the biological and chemical characteristics of a tide pool dominated by animal biomass (tide pool 2) include a slower rate of oxygen evolution with increase in irradiance (Figure 2a), low pH, and high ammonium output (Figure 3a).

#### Physical Factors

The temperature and salinity data obtained for the two natural pools confirm results from previous studies of isolated tide pools (Ganning 1971, Morris and Taylor 1983, Huggett and Griffiths 1986). Klugh (1924) stressed the importance of temperature as a limiting factor; salinity was emphasized by Newell (1970), and Ganning (cited in Newell [1970]) found that organisms commonly inhabiting tide pools can tolerate large fluctuations of salinity. In our study salinity increased only slightly (1.3‰), whereas temperature increased an average of 10°C, suggesting that temperature may be the main physical factor affecting the distribution of tide pool organisms during the midday low tides. It is important to note that these midday low tides occur only during the summer. During winter, low tides occur during the night. Therefore, the physical parameters measured in this study represent extreme highs for this local area.

#### Dissolved Oxygen

The rapid rise in levels of dissolved oxygen in tide pool 1 was caused by photosynthesis by the large population of macroalgae (Table 1). In tide pool 2, the increase in dissolved oxygen indicated net production by the small clump of the macroalga *Cladophora* and the microalgae, including the symbiotic algae in the anemones (Figure 2a). The early morning low tides left the tide pools isolated for up to several hours in the dark before sampling. The high animal biomass in tide pool 2 explains the low initial oxygen concentrations and pH. During the dark period animal respiration depletes oxygen in tide pools (Truchot and Duhamel-Jouve 1980), and increases in carbon dioxide concentration from animal respiration result in low pH of seawater (Truchot and Duhamel-Jouve 1980, Morris and Taylor 1983). It is also possible that the high  $\text{NH}_4^+$  in tide pool 2 contributed to the low pH.

#### Inorganic Nutrients

The most interesting comparison between the tide pools is the change in the inorganic nutrients within each tide pool. Tide pool 1 showed a decrease in ammonium concentration (Figure 3a); presumably this nutrient was being taken up by the algae during photosynthesis. In the same pool, nitrate and nitrite levels decreased slightly (Figure 4a), as did that of phosphate (Figure 5a). The results from tide pool 2 were completely different: ammonium increased to very high concentrations, and phosphate levels also increased (Figures 3a and 5a). This occurred in spite of the fact that the dominant animal resident of the tide pool was the symbiotic anemone *A. elegantissima*, whose zooxanthellae are expected to retain nutrients, especially in the light. Zamer and Shick (1987) found that the  $\text{NH}_4^+$  excretion rate of algae-free *A. elegantissima* was greater than that of symbiotic *A. elegantissima* in the dark, indicating that some retention of  $\text{NH}_4^+$  by the zooxanthellae may take place in this anemone. Even if  $\text{NH}_4^+$  is retained by *A. elegantissima*, our results show that an excess is released at all times. The

increase in phosphate in tide pool 2 may be a product of anemone metabolism, as previously shown by Muller-Parker et al. (1990) with *Aiptasia pallida* (Verrill), but the artificial tide pools containing only *A. elegantissima* showed little change in phosphate levels (Figure 5b), indicating that the phosphate increase in tide pool 2 must have been from some other source. The decrease in nitrate and nitrite levels in tide pool 2 was not caused by uptake by the anemones, based on the lack of change in concentration in the artificial tide pools (Figure 4b).

The higher initial concentrations of all nutrients in tide pool 2 may represent metabolites released by the anemones, with little macroalgae (relative to pool 1) to deplete seawater nutrient levels during the day. Sampling began in the artificial tide pools immediately after isolation, so initial concentrations of inorganic nutrients are those of the flow-through seawater system. Ammonium release by anemones on 7 August, 4 days after collection, was much higher than that on 10 August, 7 days after collection (Figure 3a). The difference in the amount of ammonium produced by the anemones in the artificial tide pools during the first and second set of experiments suggests that maintenance of the anemones without feeding caused a reduction in the release of ammonium. Ammonium levels in tide pool 2 (Figure 3b) showed that anemones increased the ammonium in seawater by an order of magnitude only hours after isolation of the tide pool from the ocean. Rates of ammonium production by symbiotic cnidarians vary with the host animal's diet: higher protein intake leads to higher ammonium output (Muscatine 1980, Zamer and Shick 1989, Szmant et al. 1990). The increase in the ammonium concentration of the seawater in tide pool 2 is highly suggestive that these anemones had fed recently on N-rich prey. The results also suggest that *A. elegantissima* may be an important source of dissolved inorganic nitrogen for macroalgae in tide pools.

Our study indicates that nutrients are not conserved by field populations of *A. elegantissima*. Symbiotic associations between zooxanthellae and cnidarians are predicted to

retain inorganic nutrients because the algae require these for growth (Muscatine 1980). Our work with tide pool anemone populations suggests that nutrient cycling between symbiotic algae and their animal hosts is not tightly coupled in temperate symbioses such as the *A. elegantissima* association. This provides a sharp contrast to zooxanthellae in tropical symbioses where inorganic nutrient supplies and prey are scarce. The differences between temperate and tropical symbiotic associations merit further investigation.

#### ACKNOWLEDGMENTS

We thank A. Summers for assistance with the field sampling.

#### LITERATURE CITED

- D'ELIA, C. F. 1977. The uptake and release of dissolved phosphorus by reef corals. *Limnol. Oceanogr.* 22:301-315.
- FITT, W. K., R. L. PARDY, and M. M. LITTLER. 1982. Photosynthesis, respiration, and contribution to community productivity of the symbiotic sea anemone *Anthopleura elegantissima* (Brandt, 1835). *J. Exp. Mar. Biol. Ecol.* 61:213-232.
- GANNING, B. 1971. Studies on chemical, physical and biological conditions in Swedish rockpool ecosystems. *Ophelia* 9:51-105.
- HAND, C. 1955. The sea anemones of Central California. Part II. The endomyrian and mesomyrian anemones. *Wasmann J. Biol.* 13:37-99.
- HUGGETT, J., and C. L. GRIFFITHS. 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rockpools. *Mar. Ecol. Prog. Ser.* 29:189-197.
- KLUGH, A. B. 1924. Factors controlling the biota of tide-pools. *Ecology* 5:192-196.
- MORRIS, S., and A. C. TAYLOR. 1983. Diurnal and seasonal variation in physico-chemical conditions within intertidal rock pools. *Estuarine Coastal Shelf Sci.* 17:339-355.
- MULLER-PARKER, G., C. B. COOK, and C. F.

- D'ELIA. 1990. Feeding affects phosphate fluxes in the symbiotic sea anemone *Aiptasia pallida*. *Mar. Ecol. Prog. Ser.* 60: 283–290.
- MUSCATINE, L. 1980. Uptake, retention and release of dissolved inorganic nutrients by marine algal invertebrate associations. Pages 229–244 in C. B. Cook, P. W. Pappas, and E. D. Rudolph, eds. *Cellular interactions in symbiosis and parasitism*. Ohio State University Press, Columbus, Ohio.
- MUSCATINE, L., and C. F. D'ELIA. 1978. The uptake, retention and release of ammonia by reef corals. *Limnol. Oceanogr.* 23: 725–734.
- NEWELL, R. C. 1970. *Biology of intertidal animals*. American Elsevier, New York.
- PARSONS, T. R., Y. MAITA, and C. M. LALLI. 1984. *A manual of biological and chemical methods for seawater analysis*. Pergamon Press, Oxford, England.
- STEPHENSON, T. A., A. ZOOND, and J. EYRE. 1934. The liberation and utilisation of oxygen by the population of rock-pools. *J. Exp. Biol.* 11: 162–172.
- SZMANT, A. M., L. M. FERRER, and L. M. FITZGERALD. 1990. Nitrogen excretion and O:N ratios in reef corals: Evidence for conservation of nitrogen. *Mar. Biol. (Berl.)* 104: 119–127.
- SZMANT-FROELICH, A., and M. E. Q. PILSON. 1984. Effects of feeding frequency and symbiosis with zooxanthellae on nitrogen metabolism and respiration of the coral *Astrangia danae*. *Mar. Biol. (Berl.)* 81: 153–162.
- TRUCHOT, J.-P., and A. DUHAMEL-JOUE. 1980. Oxygen and carbon dioxide in the marine intertidal environment: Diurnal and tidal changes in rockpools. *Respir. Physiol.* 39: 241–254.
- ZAMER, W. E., and J. M. SHICK. 1987. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima* II. Energy balance. *Mar. Biol. (Berl.)* 93: 481–491.
- . 1989. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima* III. Biochemical composition of tissues, substrate-specific absorption, and carbon and nitrogen budgets. *Oecologia (Berl.)* 79: 117–127.